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DIVERSITY OF SPIDERS (ARANEAE) IN A SAVANNA RESERVE, NORTHERN PROVINCE, SOUTH AFRICA

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ABSTRACT. In this study our objectives were to describe the diversity and characteristics of spider families occurring in a range of habitat types within a typical savanna ecosystem, to assess the influence of habitat type and seasonality on spider diversity and to determine levels of similarity between habitat types based on species composition. The study was conducted at Makalali Private Game Reserve, Northern Province, South Africa. Five different habitat types were sampled using four trapping techniques (sweeping, beating, active searching and pitfalls). A total of 4832 individuals including 268 species from 38 families were sampled during the study. Families showed varying degrees of habitat fidelity with some being widespread and abundant while others were restricted to a single site and were locally rare. Sites with similar habitat types showed a similarity in spider family composition. All sites have unique species compositions and overall diversity, evenness and richness of spiders do not differ with habitat type. However, analyses of functional groups, e.g., web builders and plant wanderers, showed the positive influence of structural complexity of the habitat. The presence of unique species in all habitats highlights the importance of conserving as wide array of representative habitats within ecosystems. The appearance of strong seasonal patterns in species composition also has important implications for the development of protocols for sampling species diversity. The savanna has a surprising diversity of spiders when compared to other biomes surveyed in South Africa. Factors influencing this diversity beyond the broader habitat variables measured in this study need to be investigated.

Keywords: Diversity, savanna, habitat types, seasonality, sampling techniques

In the past, invertebrates were largely ignored in conservation and only incidentally conserved in existing parks and reserves (De Wet & Schoonbee 1991). People are increasingly aware of threats to biodiversity and there is a growing need to conserve all species, not only the large vertebrates. However, meaningful conservation cannot take place if the species involved are not known (De Wet & Shoonbee 1991). Surveys of invertebrate fauna in areas where conservation strategies are already in place are especially important. Although not originally established to conserve invertebrates, the resources are already in place for the conservation of potentially new, rare and endemic invertebrate species that could exist in these areas. In addition, management plans to conserve the fauna can only be developed and implemented once inventories, or at least partial inventories are completed.

Although considerable effort has been invested in recording spider diversity in tem-

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perate habitats, only recently have studies on species diversity in tropical ecosystems been undertaken (Dippenaar-Schoeman & Jocqué 1997; Russell-Smith 1999). In South Africa most ecological studies on spiders consist of studies in agroecosystems, (Dippenaar-Schoeman 1979; Van den Berg & Dippenaar-Schoeman 1988) forest and pine plantations (Van den Berg & Dippenaar-Schoeman 1988; Van der Merve et al. 1996). Little is known about the composition of arachnid communities in savanna ecosystems, especially undisturbed conserved areas in Africa (Russell-Smith 1999). In Africa, most previous work on the inventory of savanna arachnids has been undertaken for purposes other than biodiversity assessment (e.g., Russell-Smith 1981; Van der Merwe et al. 1996). In addition, previous studies used a restricted range of sampling techniques that are likely to have provided a biased sample (Dippenaar-Schoeman 1979; Van den Berg & Dippenaar-Schoeman 1988; Dippenaar-Schoeman et al. 1999).

Inventories of faunas are essential before we can consider conservation issues and the sustainable use of our biological diversity. The present study based at Makalali Private Game Reserve, Northern Province, South Africa, has contributed to this wider survey of spider fauna in this country. The aims of this study were to investigate the spider species composition in different habitat types within a savanna ecosystem and to compare sites in terms of their family and species composition. The objectives were to: 1. describe the diversity and characteristics of families found in the different habitat types, 2. to assess the influence of habitat types and seasonality on spider diversity and 3. to produce dendrograms of similarity showing the relationships between sites and habitat types based on species composition.

METHODS

Study area.—The study was carried out at the at Makalali Private Game Reserve (29° 09′ S, 30° 42′E), a broad-leafed savanna ecosystem. Makalali is situated close to the western border of Kruger National Park and extends over 10,000 hectares. The Reserve is situated on the Lowveld plains (450 m above sea level) of Northern Province, South Africa. The two dominant vegetation types in the reserve are mixed lowveld bushveld and mopane bushveld (Acocks 1975; Low & Rebelo 1996).

The Reserve has a sub-tropical climate with a wet summer (average annual rainfall 491.5 mm) and a dry winter. The rainy season starts in October with maximum rainfall between November and February. The daytime temperature in summer months can reach as high as 36 °C. Winter evenings and mornings can be chilly (3 °C) while the days are warm (26 °C).

Spiders were sampled throughout the Reserve in five different habitat types. These were identified subjectively based on apparent differences in vegetation type and soil characteristics. The habitat types sampled were three mixed bushveld types all with different soil (fine, medium and coarse sand), mopane bushveld and rocky outcrops.

Spider sampling.—Sampling was conducted over four periods; the preliminary survey (February 1999), late summer (late February ¥ early March 1999), early summer (October–November 1999) and mid-summer (December 1999). Forty sites were surveyed throughout the reserve. Four sampling techniques (sweeping, beating, active searching and pitfall trapping) were used at all sites.

Sweeping.—A sweep net, 0.6 m in diameter with a 1.2 m long handle was swept through the grass and herb layer. Each sweep covered an arc of approximately 1.5 m through the vegetation on every alternate step (Southwood 1978). A sample consisted of two transects of 20 sweeps each, totaling 40 sweeps from each habitat type. The contents from the sweep nets were placed into a bucket with a small amount of ethyl alcohol to kill all the invertebrates. The contents were sorted on the same day and spiders and other invertebrates were separated from vegetation.

Beating.—Beating was done by firmly striking four branches (all with a diameter of greater than 2 cm) on a tree with a mallet (1.5 kg) ten times each. Eight trees, all different species, were selected randomly in all sites. In some habitat types, e.g. mopane woodland, it was not possible to sample different tree species as the habitat was dominated by a single tree species, *Colophospermum mopane*. In this case eight trees of the same species were sampled. A white beating net was held below the branches during beating. A total of 320 beats was taken from each site. The tree species,

height and diameter of the branch being beaten were recorded. The spiders were then removed from the net with a mouth suction sampler and placed into a sample jar (Sutherland 1996).

Active searching.—In February and March 1999 active searching was conducted on a catch per unit area basis. It was done by marking off two quadrats of 2 m x 2 m (8 m^2) in each habitat. Each quadrat was selected at random at least 10 m from any another quadrat. The ground, shrubs, rocks, logs and stones were thoroughly searched for spiders. Each site was searched for a total of 2 hours. In the summer samples (October–November and December 1999) the sampling protocol was changed to include eight quadrats of 1m x 1m each. This represented the same area searched (8 m^2) as before and the same amount of time (2 hours) was spent searching. It also allowed for an increase in heterogeneity into samples. Spiders were collected using either the hand to jar technique or a mouth suction sampler (Sutherland 1996). Specimens from a single quadrat at each habitat type were pooled for analysis.

Pitfall trapping.—Glass test tubes (25 mm diameter x 150 mm depth) were used as pitfall traps in each habitat. These were inserted into the ground so that the lip was flush with the soil surface and contained a 20 ml solution of 3 parts 70% ethyl alcohol and 1 part 30% glycerol (Samways 1996). The ethyl alcohol acted as a preserving agent and the glycerol prevented the ethyl alcohol from evaporating. They were arranged in two by five grids with traps placed 10 m apart. Traps were left for a period of two weeks and the contents of the pitfall traps were collected and placed into a sample bottle and later spiders were separated from the other invertebrates. Spiders were sorted into morphospecies and the other invertebrates sorted to order level.

Family-level identifications were conducted by the first and third authors while the species-level identification was done by the fourth author. The lack of taxonomic expertise in Africa within certain families, e.g. Lycosidae, makes the identification to species level in some instances impossible. Species level identifications were further hampered in the case of immature specimens and juveniles. In these cases the individuals were only identified to family and where possible to genus.

Diversity indices.—The diversity, richness, and evenness indices of spider communities were calculated using the SPDIVER.BAS program of Ludwig & Reynolds (1988). Species richness (S) examines the number of species occurring in a habitat. Just S alone, while giving insight into diversity in different habitats, can mask trends in dominance and evenness if there is no consideration of abundance. Overall species richness is the most widely adopted diversity measure. However, shifts towards incorporating species abundance has lead to widespread use of Shannon's index (H′).

A diversity index incorporates both species richness (the total number of species) and evenness (how equally abundant the species are), in a single value (Magurran 1988). A diversity index allows comparisons to be made between two habitats. One of Hill's (1973) diversity numbers (*N*1) was selected for this study: $N1 = e^{H'}$, where H′ = Shannon's index. This index is more easily interpreted than other diversity indices (Ludwig & Reynolds 1988). Given that values for diversity indices are often difficult to interpret, species richness and evenness are often presented as separate values. In this form they provide important insights into the ecological changes that occur over time or the differences between ecological communities (Bisby 1995).

When all species in a sample are equally abundant an evenness index will be at its maximum, decreasing towards zero as the relative abundance of the species diverge away from evenness. Hill's ratio (*E*5) is the least ambiguous, is the most easily interpreted and is independent of the number of species in the sample (Ludwig & Reynolds 1988).

$$E5 = \frac{(1/\lambda) - 1}{e^{H'} - 1}$$

Where: λ = Simpson's index = $({}_{i=1}\Sigma\ P_i^2)$ P_i is the proportional abundance in the *i*th species and H′ = Shannon's index.

All statistical analysis was performed using SPSS (Norusis 1994). Data were normally distributed (Kolmogorov-Smirnov test $P > 0.05$) or log transformed where necessary. A two way ANOVA was done to test for significant differences among habitat types and among the sampling period for diversity, evenness and richness.

Estimated species richness.—The estimated species richness was calculated to determine whether or not the environment had been sufficiently sampled. The Choa 1 estimate was calculated (Colwell & Coddington 1994).

$$S_{Choa\ 1} = S_{obs} + F_1^2 / 2F_2$$

Where: S_{obs} = species observed; F_1 = number of singletons; F_2 = number of doubletons. The Estimate S program (Colwell 2000) was used for the calculation and to generate the data for the species accumulation curves.

Spider functional groups.—Functional groups include species that potentially compete for jointly exploited limited resources (Polis & McCormick 1986). Spiders live in a well defined environment with limitations set by both physical conditions and biological factors (Foelix 1996). They can be grouped into specific functional groups based on available information on their habitat preferences and predatory methods (Bultman et al. 1982). Describing the spider diversity in terms of these groups allows for greater insight into how habitat differences may be reflected in life history strategies. For the present study three main functional groups were recognized, namely plant wanderers (PW), ground wanderers (GW) and web builders (WB), with further subdivisions based on microhabitat and general behavior (Dippenaar-Schoeman et al. 1999).

Similarity analysis.—The degree of association or similarity of sites or samples was investigated using standard ecological techniques of ordination and classification (Southwood 1978). Ordination techniques are frequently used to investigate the overall similarity of sites and establish major groupings.

The term "cluster analysis" encompasses a number of different classification algorithms (Faith 1991). It is a useful data reduction technique that can be helpful in identifying patterns and groupings of objects. The analysis begins with each object in a class by itself (StatSoft 1999). The threshold regarding the decision when to declare two or more objects to be members of the same cluster is lowered. As a result more and more objects are linked together and aggregate (amalgamate) into larger and larger clusters of increasingly dissimilar elements. A dendrogram results and the horizontal axis denotes the linkage distance (Faith 1991; StatSoft 1999). Clusters (branches) resulting from the analysis can be detected and interpreted (StatSoft 1999).

The statistical analysis program STATISTICA (StatSoft 1999) was used to generate dendrograms. The unweighted pair group average linkage and the Euclidean distances were the parameters selected. The analysis was done using 1. families and 2. species present in the different sites.

RESULTS

Total numbers of species and individuals.—A total of 4 832 individuals from 268 species, 147 genera and 38 families was sampled in Makalali Private Game Reserve during the study period. Table 1 is a summary of the species composition. Voucher specimens were preserved in 70% ethanol and deposited in a reference collection lodged with the Natural Science Museum, South Africa (Accession numbers: DMSA–ARA 346–611). A checklist of spiders collected in this study is presented in Whitmore et al. (2001).

Some families were more widely distributed throughout the Reserve while others were restricted to one or a few habitat types. Two families found at all sites were lynx spiders (Oxyopidae) and jumping spiders (Salticidae). Three families were found in 98% of the sites: nursery web spiders (Pisauridae), orb-web spiders (Araneidae) and crab spiders (Thomisidae). Other families found in more than 75% of all sites included comb-footed spiders (Theridiidae), flat-bellied ground spiders (Gnaphosidae), small huntsman spider (Philodromidae), sac spiders (Miturgidae), large huntsmans spiders (Sparassidae) and wolf spiders (Lycosidae).

Families that were only found at a single site included: six-eyed tunnel spiders (Segestriidae); velvet spiders (Eresidae); six-eyed spiders (Sicariidae); dwarf ring-shield spiders (Anapidae); net-casting spiders (Deinopidae); mesh-web spiders (Dictynidae); funnel-web spiders (Agelenidae) and spurred trapdoor spiders (Idiopidae). It must be noted that although these families were found at only one site, the species were not necessarily rare. They may be cryptic or have a patchy distribution and thus may not have been adequately sampled.

Diversity, evenness and richness indices.—There was no overall significant differ-

Table 1.—Total numbers of spider families, genera, species and individuals sampled from Makalali Private Game Reserve. GW = ground wanderers, PW = plant wanderers and WB = web builders. 1 = white sandy bushveld, 2 = general bushveld, 3 = brown sandy bushveld, 4 = rocky outcrops and 5 = mopane woodland). Numbers in parentheses represent the total number of individuals collected.

Functional group	Family	Genera	Total species	Habitat type 1	2	3	4	5
GW	Gnaphosidae	8	14	9 (25)	9 (24)	6 (23)	7 (38)	8 (37)
	Lycosidae	6	16	7 (13)	10 (19)	4 (16)	4 (7)	8 (18)
	Zodariidae	5	9	2 (2)	3 (3)	1 (1)	2 (2)	5 (6)
	Theraphosidae	4	4	1 (2)	2 (7)	3 (11)	2 (7)	2 (4)
	Caponiidae	1	1					1 (1)
	Corinnidae	3	6	2 (2)	2 (2)	3 (4)	1 (1)	2 (5)
	Ctenidae	3	4	1 (3)	1 (2)	2 (2)	2 (3)	1 (1)
	Prodidomidae	3	2	3 (6)	1 (13)		2 (3)	1 (5)
	Liocranidae	2	2	1 (3)	1 (3)	2 (2)	1 (1)	
	Oonopidae	2	2			1 (1)	1 (1)	1 (1)
	Palpimanidae	2	3		1 (1)	1 (2)	3 (4)	2 (3)
	Selenopidae	2	2					
	Agelenidae	1	1		1 (2)			
	Anapidae	1	1				1 (2)	
	Barychelidae	1	1		1 (1)	1 (2)		1 (1)
	Dictynidae	1	1			1 (1)		
	Idiopidae	1	1	1 (3)				
	Scytodidae	1	3		2 (2)	2 (3)	2 (2)	3 (4)
	Sicariidae	1	2				1 (1)	
PW	Salticidae	15	32	16 (152)	18 (140)	20 (284)	23 (189)	18 (66)
	Thomisidae	15	27	17 (84)	18 (94)	16 (111)	23 (68)	22 (54)
	Philodromidae	5	9	7 (38)	4 (40)	7 (31)	5 (18)	6 (38)
	Pisauridae	5	11	5 (35)	9 (50)	8 (85)	7 (102)	6 (35)
	Oxyopidae	3	19	11 (77)	13 (53)	16 (80)	14 (49)	13 (31)
	Sparassidae	3	5	3 (44)	4 (26)	3 (17)	4 (28)	5 (16)
	Miturgidae	2	7	7 (33)	9 (52)	5 (30)	5 (17)	5 (16)
	Clubionidae	1	2	1 (6)	1 (2)	12 (1)	1 (5)	1 (5)
WB	Araneidae	18	31	14 (437)	19 (242)	20 (196)	22 (288)	18 (317)
	Theridiidae	10	28	8 (60)	14 (58)	17 (75)	13 (106)	13 (32)
	Hersiliidae	2	3	1 (1)	1 (1)	3 (17)	2 (3)	
	Linyphiidae	2	6	1 (1)	3 (5)	1 (3)	2 (5)	3 (3)
	Pholcidae	2	3	1 (1)	1 (1)	1 (1)	1 (1)	1 (1)
	Tetragnathidae	2	3	1 (11)	1 (3)	1 (15)	2 (12)	1 (35)
	Uloboridae	2	3	1 (5)	1 (2)	1 (4)	1 (3)	
	Deinopidae	1	1			1 (1)		
	Eresidae	1	2				1 (1)	
	Nesticidae	1	1			1 (4)		
	Segestriidae	1	1					1 (1)
TOTAL	37	147	268	121 (1044)	150 (848)	160 (1034)	155 (967)	148 (736)

ence between the diversity ($F_{4, 39} = 2.236$, $P = 0.094$), evenness ($F_{4, 39} = 1.689$, $P = 0.184$) or richness ($F_{4, 39} = 1.766$, $P = 0.167$) among the different habitat types (Figs. 3a, b & c). When analyzed by sampling period there was a significant difference for the diversity ($F_{2, 39} = 16.779$, $P < 0.0001$; Fig. 4a) and richness ($F_{2, 39} = 10.253$, $P = 0.001$; Fig. 4b) but the results were non-significant for evenness ($F_{2, 39} = 2.461$, $P = 0.106$; Fig. 4c). The diversity and richness follow the same patterns throughout the year, both being highest in midsummer (December). The interaction between the sampling period and habitat type was non-significant for diversity ($F_{8, 39} = 1.157$, $P = 0.362$), richness ($F_{8, 39} = 1.408$, $P = 0.242$) and evenness ($F_{8, 39} = 0.848$, $P = 0.571$). The diversity, evenness and richness

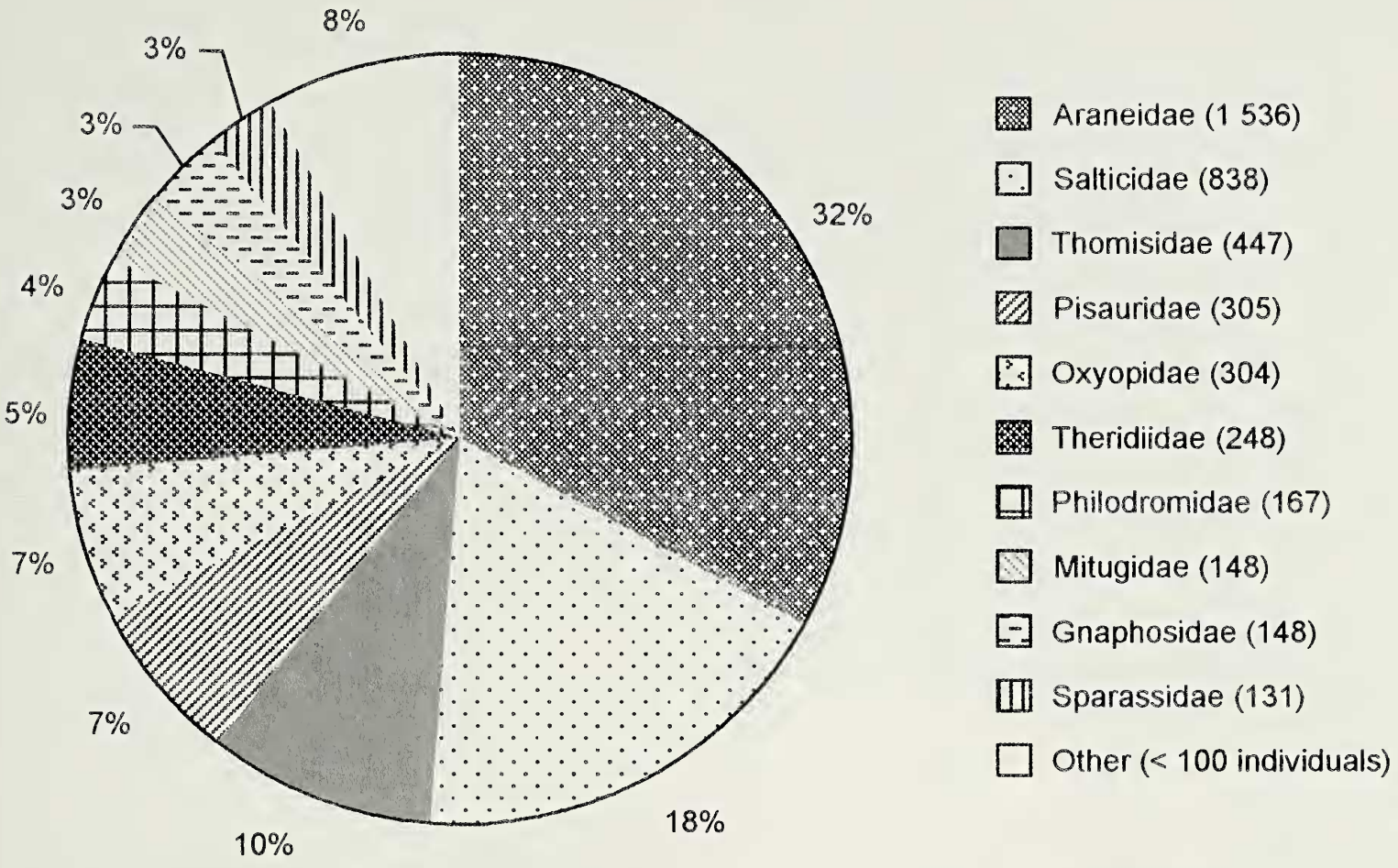

Figure 1.—Family level diversity of spiders at Makalali Private Game Reserve. Percentage abundance of the different spider families (parentheses indicate the number of individuals). The following families have been included in the "other" category Tetragnathidae (75); Lycosidae (71); Theraphosidae (31); Clubionidae (30); Hersiliidae (21); Prodidomidae (19); Uloboridae (17); Linyphiidae (17); Zodariidae (14); Corinnidae (14); Scytodidae (11); Ctenidae (11); Palpimanidae (10); Liocranidae (9); Pholcidae (5); Nesticidae (4); Barychelidae (4); Oonopidae (3); Idiopidae (3); Agelenidae (3); Anapidae (2); Sicariidae (1); Segestriidae (1); Eresidae (1); Dictynidae (1) and Deinopidae (1).

follow the same patterns in the different habitat types at different times of the year i.e. times when diversity is high so was the evenness and richness.

Functional groups and families.—Spiders were divided into three main functional groups: the plant wanderers, ground wanderers and the web-builders. The diversity, richness and evenness values were reassessed at this level to determine if the different life strategies of spiders are influenced in any way by the habitat and or by time as these patterns may be masked by the overall effect of a combined diversity.

Overall, the number of wandering spiders was greater than that of web builders. Plant wanderers were the most abundant and widely distributed. They comprised 48% of all spiders sampled (total individuals = 2239). Web builders comprised 41% (total individuals = 1916) and ground wanderers, 11% (total individuals = 501). The diversity of web- builders was significantly affected by habitat type ($F_{4,39} = 3.452$, $P = 0.022$) but the plant wanderers ($F_{4,39} = 0.217$, $P = 0.927$) and ground wanderers ($F_{4,39} = 0.368$, $P = 0.829$) were not (Fig. 5a). The richness was not significantly affected by habitat type for any of the spider functional groups (plant wanderers: ($F_{4,39} = 0.226$, $P = 0.921$), ground wanderers: ($F_{4,39} = 0.898$, $P = 0.480$) and web builders: ($F_{4,39} = 2.243$, $P = 0.093$)) (Fig. 5 b). Similarly the evenness for plant wanderers ($F_{4,39} = 2.735$, $P = 0.051$), ground wanderers ($F_{4,39} = 0.521$, $P = 0.721$) or web builders ($F_{4,39} = 0.491$, $P = 0.743$) was not significantly effected by habitat type (Fig. 5c).

The effect of sampling period on community structure differed slightly from the results for the combined analysis (see previous section). The diversity of plant wanderers was not significantly affected by the sampling period ($F_{2,39} = 1.405$, $P = 0.268$; Fig. 6a) yet the richness ($F2_{,39} = 3.803$, $P = 0.036$) and evenness ($F_{2,39} = 5.482$, $P = 0.011$) were (Figs. 6b & c). The diversity ($F_{2,39} = 15.797$, $P < 0.001$) and richness ($F_{2,39} = 21.102$, $P < 0.001$) of ground wanderers was significantly

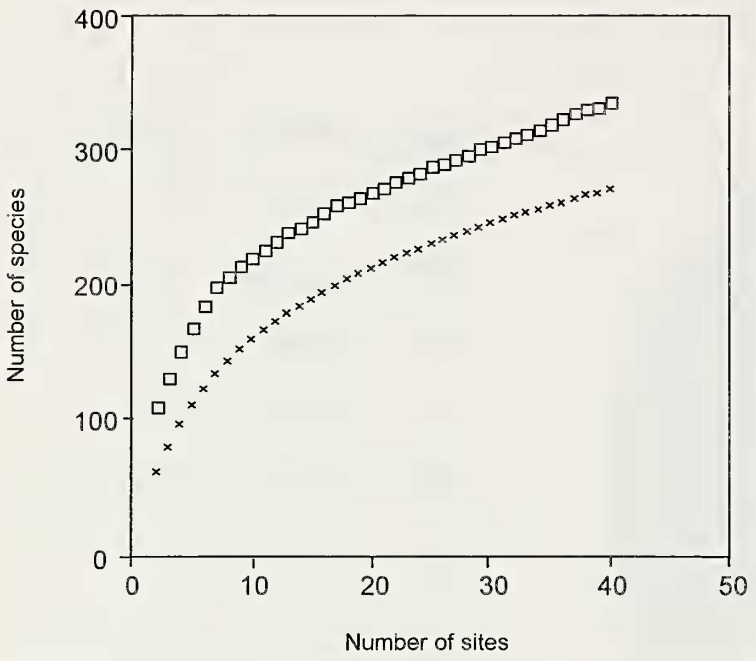

Figure 2.—The observed (□) and estimated (✖) species richness for the five different habitat types based on the Choa 1 estimators.

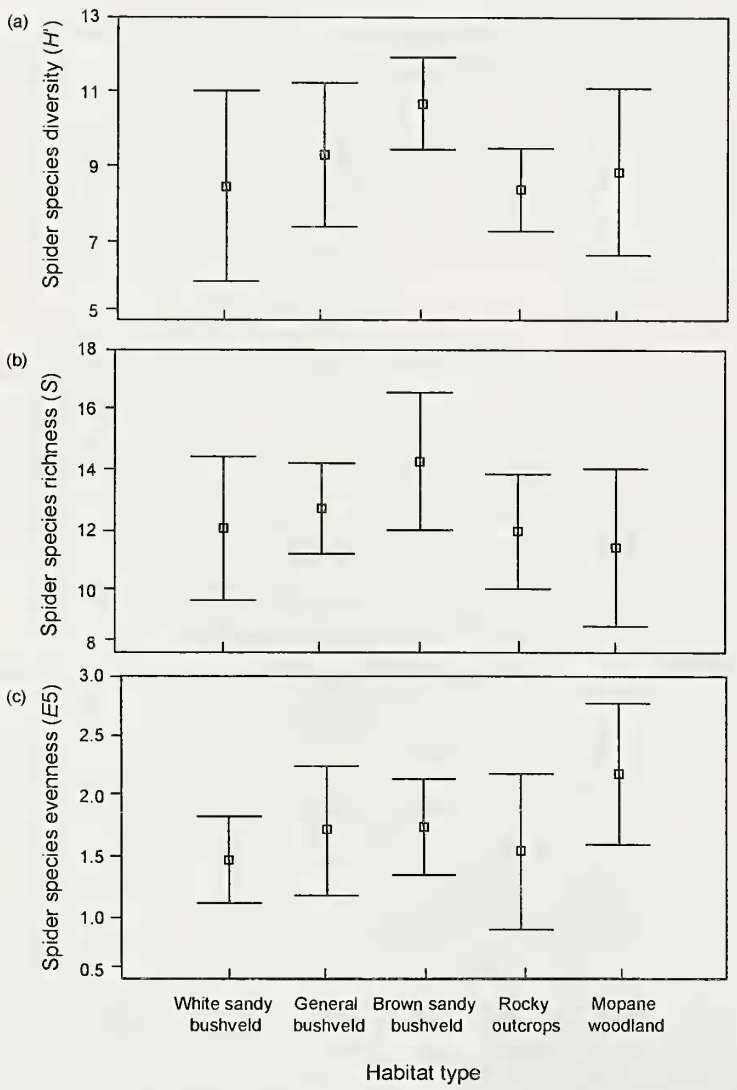

Figure 3.—The influence of habitat type, represented by the mean and ± 95% confidence limits on the a) species diversity, b) species richness and c) species evenness of spiders at Makalali Private Game Reserve. Sample size is eight in each habitat type. There were no statistically significant differences (see text).

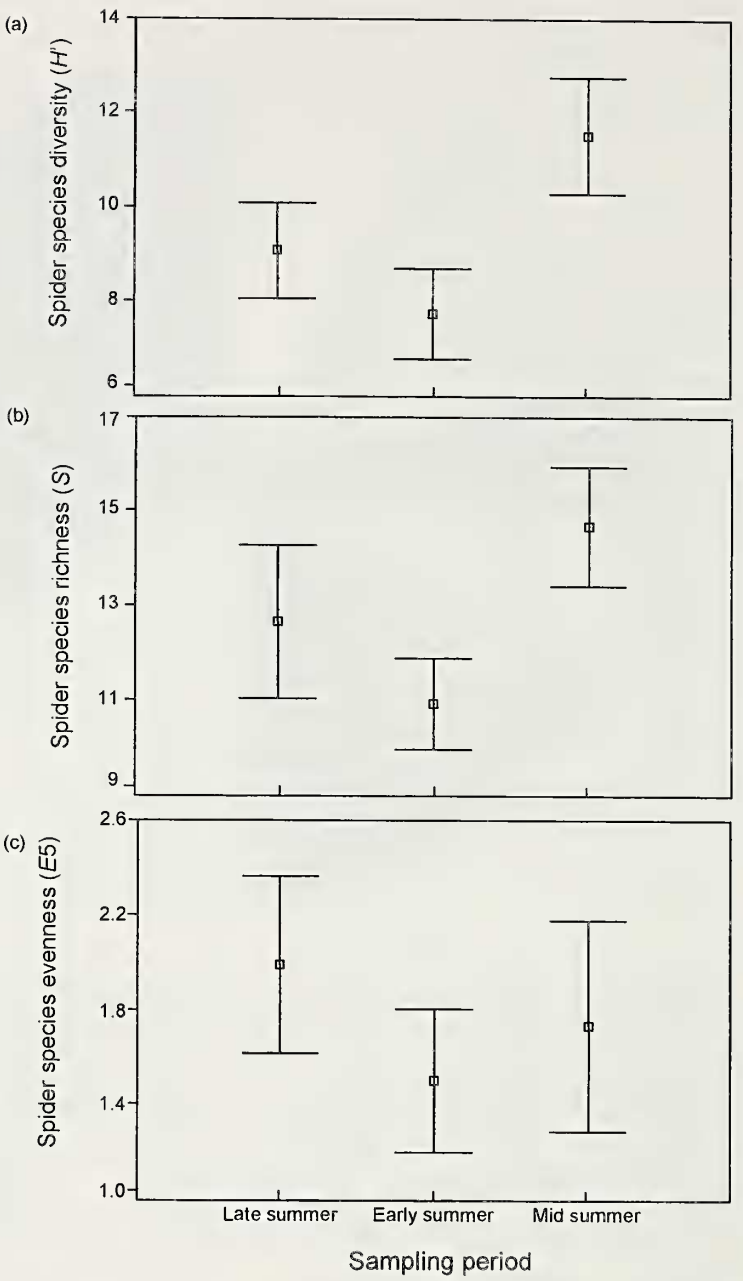

Figure 4.—The influence of sampling period, represented by the mean and ± 95% confidence limits on the a) species diversity, b) species richness and c) species evenness of spiders at Makalali Private Game Reserve. See text for statistical tests.

affected by the sampling period but the evenness ($F_{2,39}$ = 0.721, P = 0.447) was not (Figs. 6a, b &c). The diversity ($F_{2,39}$ = 10.013, P = 0.001) and richness ($F_{2,39}$ = 5.390, P = 0.011) of web builders was significantly affected by the sampling period but the evenness ($F_{2,39}$ = 1.067, P = 0.359) was not (Figs. 6a, b & c).

Interestingly, there was no overall significance between the evenness and sampling period but when spiders were divided into functional groups, there is an evenness effect with time on plant wanderers. This indicates that at different times of the year different compliments of ground wanderer and web building species are dominating the environment and the abundance of these species is relatively uniformly distributed. This means for ground wanderers and web builders we are either

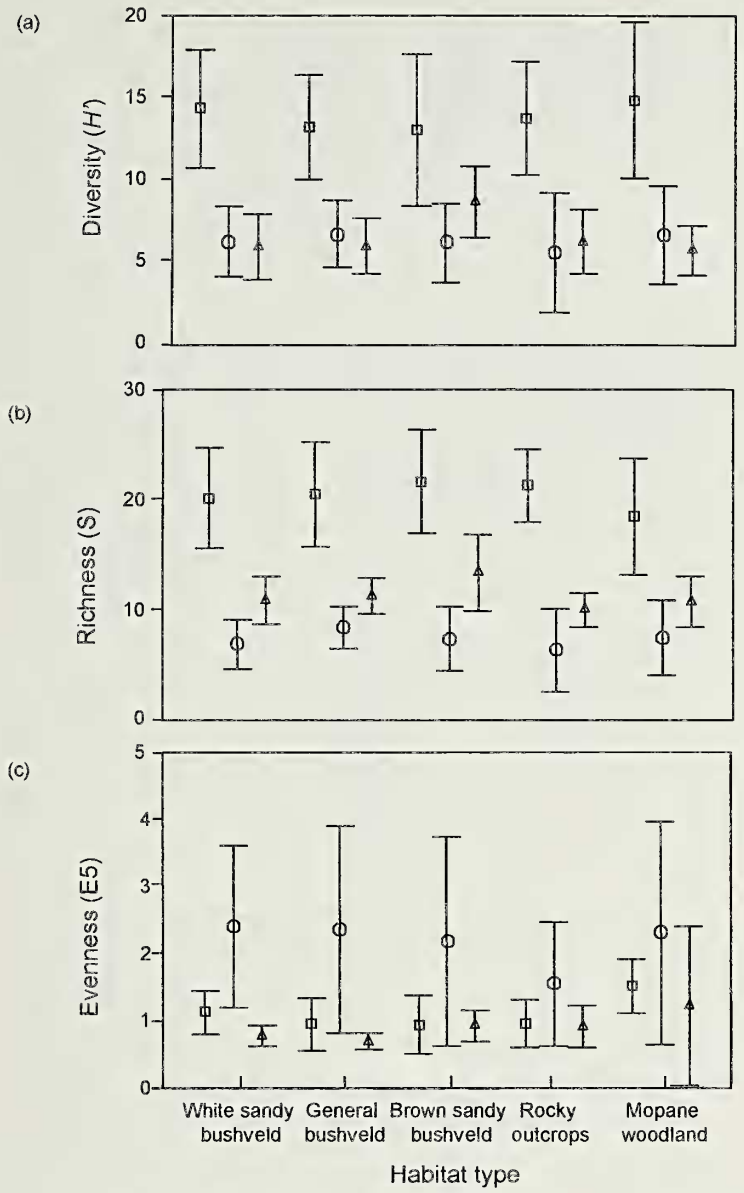

Figure 5.—The effect of habitat type on the a) diversity, b) richness, and c) evenness of spiders at Makalali Private Game Reserve. Spiders have been divided into plant wanderers (□), ground wanderers (○) and web builders (△). The mean and 95% confidence limits are presented. Sample size is eight in all habitat types.

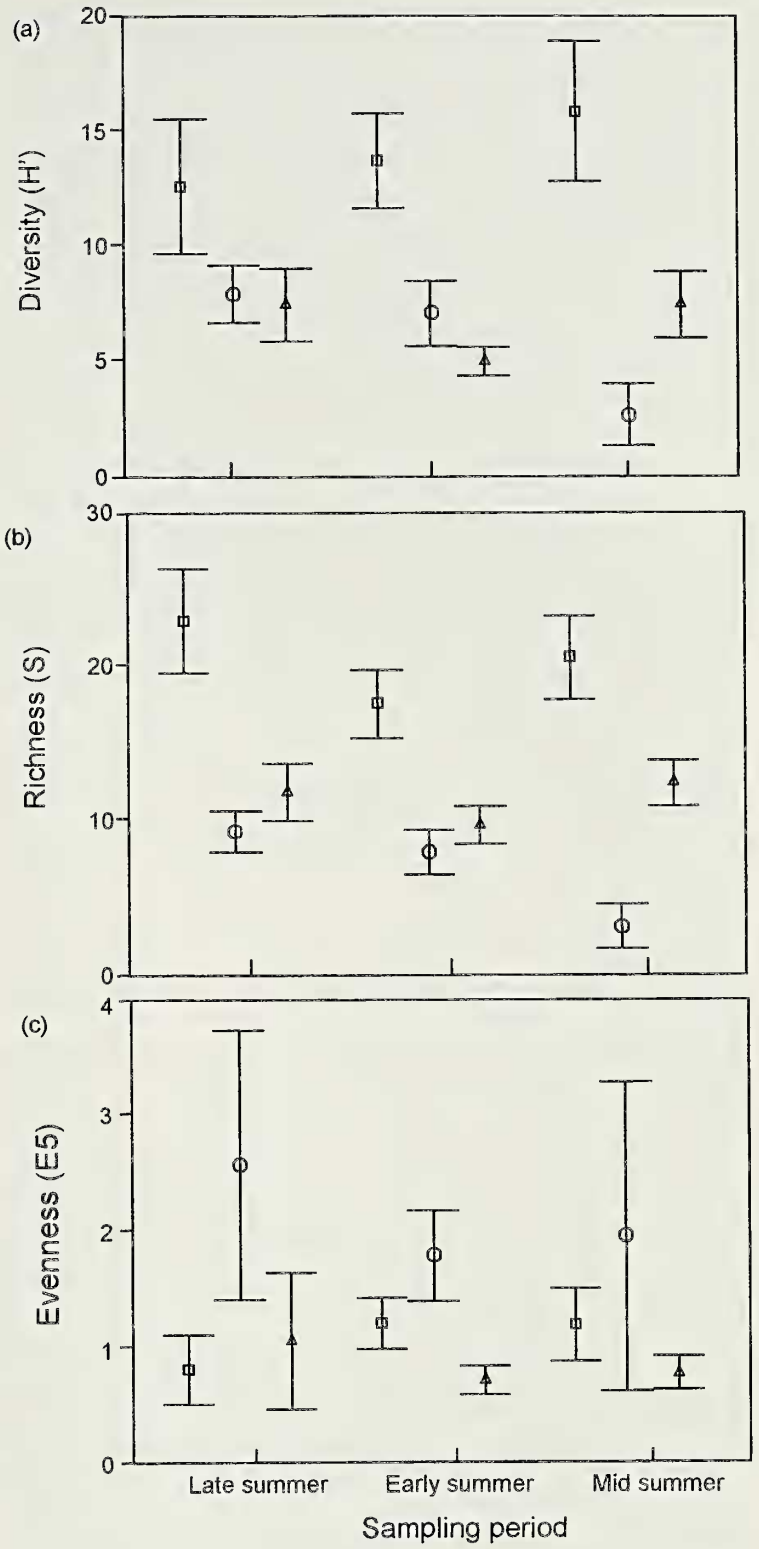

Figure 6.—The effect of sampling period on the a) diversity, b) richness, and c) evenness of spiders at Makalali Private Game Reserve. Spiders have been divided into guilds: plant wanderers (□), ground wanderers (○) and web builders (△). The mean and 95% confidence limits are presented. The sample size is 15 for late and early summer and 10 for mid summer.

sampling many individuals of the same species or few individuals of many different species at any particular time of the year.

The difference in evenness for plant wanderers with season may be influenced by the structural diversity of the habitat or spider phenology. Therefore, either the plant wanderer evenness is highest when there is maximal structural diversity (mid summer) or at different times of the year there are numerous juveniles of one species and at other times of the year fewer adult individuals of the same species. The only way to get a true habitat type effect on the diversity would be to resample the same sites at the different times of the year.

Similarity analysis.—The family level analysis revealed three main clusters (Figs. 7 & 8a). Cluster A had two sites, 4.6 and 1.3. Cluster B consisted of a combination of habitat types 3, 4 and 5 while cluster C was a combination of mainly habitat types 1 and 2 with two sites from habitat type 3 (Fig. 8a). At the species level there were four distinct clusters (Figs. 7 & 8b). Each cluster had sites from at least four different habitat types (Fig. 8b). At first there did not appear to be any

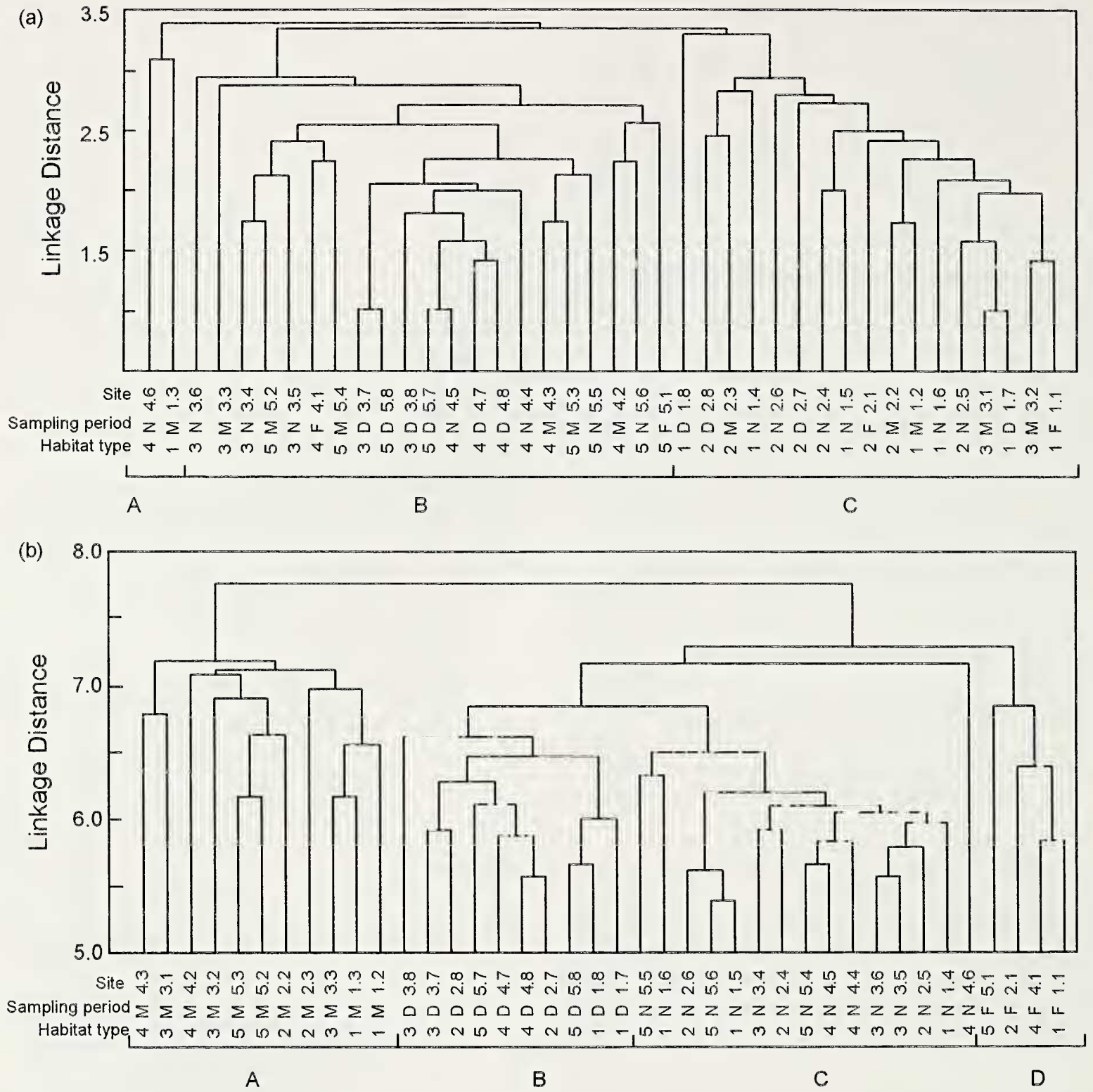

Figure 7.—Dendrogram for a) families and b) species shared at different habitat types and different sampling times sites using the unweighted pair-group average (UPGAMA) and Euclidean distances. There are three main clusters (A–C) of sites for shared families. These cluster at a habitat level. Four main clusters (A–D) are present for species shared and these cluster according to season. Sampling sites are coded by habitat type (1 = white sandy bushveld, 2 = general bushveld, 3 = brown sandy bushveld, 4 = rocky outcrops, and 5 = mopane woodland with the site number within the habitat after the sampling period. The letters represent the sampling period where M = late summer (March 1999), N = early summer (November 1999), D = mid summer (December 1999) and F = preliminary sample (February 1999).

pattern. The same data were re-analyzed using the sampling period (i.e. time of year) instead of sites. The results showed that sites clustered according to sampling period. Cluster A was the autumn sample (March 1999), Cluster B was the summer sample (December), Cluster C was the spring sample (October 1999) and Cluster D was a late summer sample, taken during the preliminary survey in February 1999 (Figs. 7b & 8c).

DISCUSSION

Species composition.—The 38 spider families recorded from Makalali Private Game Reserve represent 60% of all currently recognized spider families in South Africa (Dip-

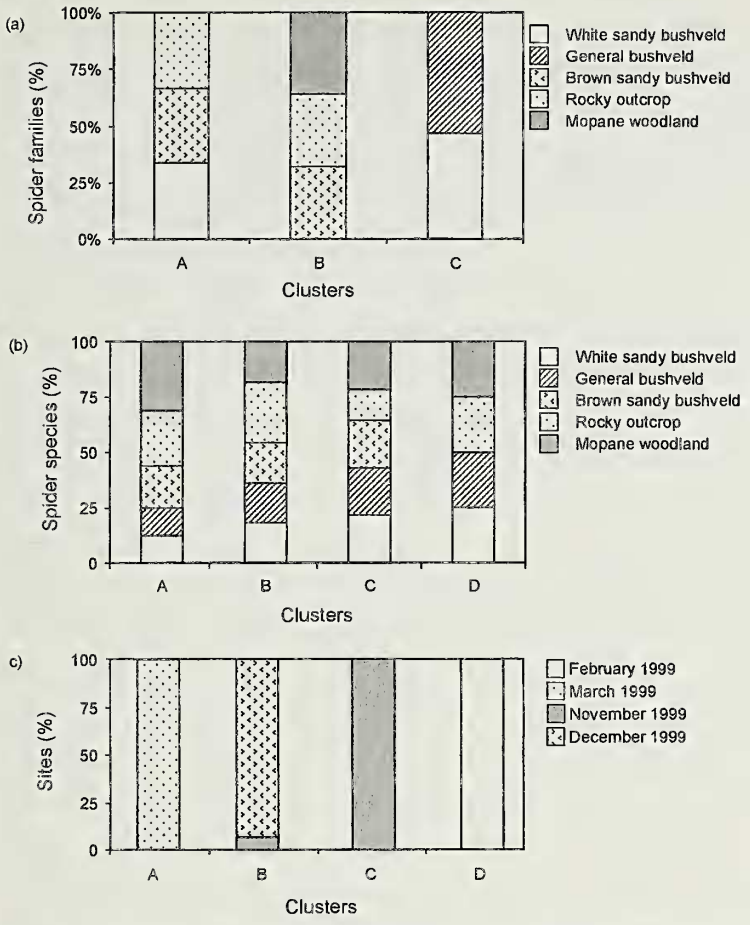

Figure 8.—The percentage of (a) families in clusters A–C, (b) species in clusters A–D and (c) the species clusters A–D according to sampling period. The clusters (A–D) correspond with those of Figure 7.

penaar-Schoeman & Jocqué 1997). The most striking result is the surprisingly high diversity in this savanna biome compared with other biomes that have been surveyed in South Africa. The number of families found here is as high or higher than numbers recorded for other biomes surveyed in South Africa (see Table 3 in Whitmore et al. 2001). Only one study done in the Nama-Karoo (Dippenaar-Schoeman et al. 1999) showed family richness equal to that in our current study. However, that study was conducted over a ten year period and sampling for the present study was done in a single year. The spider family diversity in this savanna biome was therefore surprisingly high (Whitmore et al. 2001). This study illustrates that savanna biomes are very important for the preservation of invertebrate biodiversity and are thus an essential biome to conserve. Furthermore, this study indicates that previous studies of other biomes in South Africa may not be complete. The estimated richness values indicate that even the considerable effort invested in this study failed to sample all the fauna. The families that were abundant were also widely distributed throughout the Reserve. Some families were not as cosmopolitan and were only found in a single site. Site restriction by some species should not be confused with rarity. Many of these species are cryptic or patchily distributed and were not sampled adequately. Some examples include *Stegodyphus dumicola* Pocock 1898 and the baboon spiders (e.g., *Ceratogyrus bechuanicus* Purcell 1902 and *Pterinochilus nigrofulvus* (Pocock 1898)). *Stegodyphus dumicola* was only sampled in one habitat type but the distribution is known to be extremely patchy (Siebt & Wickler 1988). Numerous nests were observed outside of the immediate sampling areas. This particular group may not have been sampled adequately because of its patchy distribution and not because the species is rare. The theraphosids (baboon spiders) were sampled from all five different habitat types but in low abundances (only 15 individuals were found throughout the Reserve). Low trap catches may be a reflection on an inadequate sampling protocol for this particular taxon. Theraphosids are nocturnal and in this study night sampling was not done. However, additional hand collecting was done and three different theraphosid species were collected from their burrows. These additional species were not found while sampling in the sites. Many theraphosid burrows were observed, especially in the western section of the Reserve in the white sandy and brown sandy mixed bushveld habitats (habitat types 1 and 2).

Diversity, evenness and richness.—There are many environmental factors that affect species diversity. Some of these factors include: 1. seasonality, 2. spatial heterogeneity, 3. competition, 4. predation, 5. habitat type, 6. environmental stability and 7. productivity (Rosenzweig 1995). If spider family distribution was affected by a single factor, e.g. the habitat type, we would expect all sites within a habitat type to have high similarity values and share little with other sites.

Diversity values varied considerably between the different sites and similar habitat types did not necessarily have similar diversities. There was no overall significant difference between the diversity, evenness or richness among the different habitat types. This is surprising because we would expect bushveld habitat types (types 1–4), a combination of different trees, herbs and shrubs (structurally

complex), to have a higher diversity than the mopane woodland habitat type as this habitat type is dominated by a single tree species (*Colophospermum mopane*). However, this was not the case and although the mopane woodland appears to be a more barren habitat (floristically) it still has a high spider diversity.

The results indicate that all sites have unique species compositions. Additionally, there are many factors that determine the species composition at a site and not simply the habitat type. An alternative interpretation of this is that the habitat types classified as different at the start of the study may be more similar than previously thought.

However, when spiders were divided according to their functional group there was a significant effect of habitat on the diversity of web builders and the evenness of plant wanderers. The web building and plant wandering spiders rely on vegetation for some part of their lives, either for finding food, building retreats or for web building. The structure of the vegetation is therefore expected to influence the diversity of spiders found in the habitat. There were many more plant wanderers and web builders sampled than ground-dwellers. This again indicates that structural diversity of the vegetation may, in some way, influence the spider diversity.

Studies have demonstrated that a correlation exists between the structural complexity of habitats and species diversity (Uetz 1979; MacArthur 1964; Pickett et al. 1991; Andow 1991; Hawksworth & Kalin-Aroyo 1995; Rosenzweig 1995). Diversity generally increases when a greater variety of habitat types are present (MacArthur 1964; Ried & Miller 1989; Cook 1991; Hawksworth & Kalin-Arroyo 1995).

Uetz (1991) suggests that structurally more complex shrubs can support a more diverse spider community. Downie et al. (1999) and New (1999) have demonstrated that spiders are extremely sensitive to small changes in the habitat structure, including habitat complexity, litter depth and microclimate characteristics. Generally, as disturbance increases the spider species richness decreases. Thus the physical structure of environments has an important influence on the habitat preferences of spider species, especially web-building species (Uetz 1991; Hurd & Fagon 1992).

All habitat types have unique families and species indicating that all habitats are important if the spider biodiversity is to be conserved. Therefore, no one habitat type is less important than another and efforts should be made to conserve representatives of all habitat types within the Reserve. Habitat type seems to influence the spider composition at the family level because similar families cluster within a similar habitat type. However, for species, the habitat type does not seem to affect the community composition. According to the cluster analysis, the results at the level of species closely corresponded to the sampling periods. This indicates that similar species are present at specific times of the year. Thus, at the scale measured, seasonal variation may be a more important determinant than the habitat type alone. This provides valuable insight into sample protocols and certain species may dominate at different times of the year. Therefore, to get a true representation of the species present sampling should be conducted in all seasons. This conclusion is supported by other work being conducted in the Reserve on other invertebrates (beetles, ants and grasshoppers) where different species dominated at different times of the year. In addition, certain species may mature at different times of the year and thus by conducting sampling throughout the year adults can be collected. The adults are taxonomically important, as they are often essential for species level determinations.

The savanna habitat has a surprisingly diverse spider community and further research should be encouraged in this biome. However, to maintain and manage this high diversity factors other than habitat type need to be identified. Factors at the microhabitat scale, which may be important in influencing the diversity, need to be investigated.

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